1 An overview of tapeworms from vertebrate bowels of the earth

By
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INTRODUCTION

In these times, it is rare that those who study Natural History are presented with an opportunity to take a global look at the diversity of any taxonomic group. This is extremely regrettable given this approach has been employed to such great advantage in centuries past by numerous distinguished naturalists, including, for example, Charles Darwin and Alfred Russel Wallace, whose discoveries ultimately served as the foundation of disciplines such as Evolution, Ecology, Biogeography, and Biodiversity, to name just a few. The demands and time restrictions of contemporary academia are among the factors contributing to the decline in such global work today, but the situation is exacerbated by limitations in funding. Based on the enthusiasm we experienced over the course of this project from all corners of the world, the decline is most decidedly *not*, the result of a lack of interest!

In an attempt to remedy the situation, in 2003, the National Science Foundation (NSF), in partnership with the ALL Species Foundation, and the Alfred P. Sloan Foundation, established the Planetary Biodiversity Inventories (PBI) program. This program was aimed at funding species-level inventories of major groups of organisms *across the planet*. For the relatively brief period of its existence, the PBI program did much to restore enthusiasm for exploring biodiversity on a global scale. In 2008, in the last year of the program, our project: ***A survey of tapeworms from vertebrate bowels of the earth*** was funded. For the next eight years, our international team scoured the earth discovering and describing tapeworms (i.e., cestodes) from birds, mammals, frogs, lizards, snakes, bony fishes, and elasmobranchs (i.e., sharks and stingrays). As mandated by NSF, the project also included substantial training and outreach activities. It is not an overstatement to say that this funding from the PBI program changed tapeworm systematics forever—transforming it into the synthetic discipline it is today. Lest the impact of this remarkable investment in this poorly known, and in fact often maligned, group of parasites be lost among the many other valuable endeavors funded by NSF, our project team collaborated to generate this Special Issue. It is our hope that in assembling the results of our activities and discoveries into a single document, the full magnitude and value of this creative program will not go unrecognized. It is also our hope that this document will serve to catalyze future work on this intriguing group of parasitic platyhelminths.

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PROJECT GOALS

The overall objective of the project was to provide a global synthetic treatment of the diversity, classification, morphology, host associations, geographic distribution, and interrelationships of cestodes. To this end, the project had six primary goals. (1) To discover and describe as much cestode novelty as possible by examining a wide array of species of vertebrates from as many different countries as possible across the globe that had not previously been examined for cestodes. (2) To recollect from historically problematic regions and/or host taxa to resolve major outstanding taxonomic issues. (3) To collect specimens of as many different cestode species across as great a diversity of cestode taxa as possible and preserve them for novel morphological and molecular work. (4) To assess interrelationships at multiple levels based on phylogenetic analyses of molecular sequence data from multiple genes informed by morphological data. (5) To attempt to reconcile cestode classification at all levels with a revised understanding of their phylogenetic relationships. (6) To use historical data and new collections to begin to generate estimates of total global diversity for at least a subset of cestode orders.

THE TEAM

As Principal Investigators (PIs) of the project, Janine Caira (University of Connecticut) and Kirsten Jensen (University of Kansas) were responsible for overall project management. Co-Principal Investigator (Co-PI) Tim Littlewood and postdoctoral fellow Andrea Waeschenbach (The Natural History Museum, London) coordinated the molecular work. Co-PI Jean Mariaux (Muséum d'Histoire Naturelle de Genève) coordinated the ultra-speciose cyclophyllidean elements of the project. In total, over 250 individuals worked on the project in various roles; these are detailed below.

Given that tapeworm systematists self-organize by their cestode orders of interest, and thus also by the vertebrate classes parasitized by their cestode orders of interest, project personnel were assembled into four "host" teams. Each team was led by one to three taxonomists with expertise in the groups of cestodes that parasitize her/his/their particular host group. The *bird-hosted* cestode team was led by Jean Mariaux (Muséum d'Histoire Naturelle de Genève) and Boyko Georgiev (Bulgarian Academy of Sciences), the *mammal-hosted* cestode team by Vasyl Tkach (University of North Dakota), the *bony fish-hosted* cestode team by Tomáš Scholz and Roman Kuchta (both Czech Academy of Sciences), and Alain de Chambrier (Muséum d'Histoire Naturelle de Genève)—this team was also responsible for the holocephalan (ratfish) cestodes; the *elasmobranch-hosted* cestode team was led by Janine Caira and Kirsten Jensen. The dearth of cestodes reported from frogs, snakes, lizards, and their kin did not justify a separate team to cover the cestodes of these host groups, instead given that the cestode groups hosted by these vertebrates are the same as those hosted by bony fishes, Alain de Chambrier of the fish-cestode hosted team led the work on cestodes from herptiles.

Team leaders formulated and implemented the strategy for treating their respective cestode order(s). Each chose to enlist the assistance of additional taxonomic experts from across the globe. By host group, these experts included for *mammals*: Ian Beveridge (University of Melbourne), Voitto Haukisalmi (Forest Research Institute, Finland), and Vadim Kornyushin (National Academy of Sciences, Ukraine); *birds*: Eric Hoberg (Smithsonian Institution), Vadim Kornyushin (National Academy of Sciences, Ukraine), Pavel Nikolov (Bulgarian Academy of Sciences), Gergana Vasileva (Bulgarian Academy of Sciences); *bony fishes*: Alicia A. Gil de Pertierra (University of Buenos Aires), and Vladimíra Hanzelová and Mikulas Oros (Slovak

Academy of Sciences); *elasmobranchs*: Ian Beveridge (University of Melbourne), the late Louis Euzet (France), Claire Healy (Royal Ontario Museum), Verónica Ivanov (Universidad de Buenos Aires), Masoumeh Malek (University of Tehran), Fernando P. L. Marques (Universidade de São Paulo), Lassad Neifar (Faculté des Sciences de Sfax, Tunisia), Harry Palm (Universität Rostock), Florian Reyda (State University of New York at Oneonta), and Timothy Ruhnke (West Virginia State University). Each "host" team also generally included at least one to two postdoctoral fellows, as well as multiple graduate and undergraduate students. Additional detail on these individuals is provided in the Training section below.

A program assistant, Elizabeth Barbeau, supported in part with matching funds to this award from the University of Connecticut (UConn), was responsible for all clerical aspects of the project and was also heavily involved in the development and population of the project databases. The project website and databases were developed in collaboration with Yi Zhang, Josh Roy, and Jason Card from UConn's University Information Technology Services (UITS). The children's book *Meet the Suckers* was also a collaborative effort involving Virge Kask of UConn (backgrounds), Joachim Mohrenberg of Braunschweig, Germany (cartoons of children; http://www.mohrenberg.de/), and Elizabeth Barbeau (content design). The original cover art for this Special Issue was done by Kendel Craig, the winner of a competition we held with the design students of the American School in London, for this honor.

Collaboration across "host" teams was greatly facilitated by annual project meetings held in Geneva in 2009 and 2012, Melbourne in 2010 (following the International Congress of Parasitology), Kansas in 2011, London in 2013, and Brazil in 2014. The meetings in 2011 and 2014 coincided with the 7th and 8th International Workshops on Cestode Systematics, respectively. The former Workshop was largely funded by the PBI project and was organized by PI Jensen at the University of Kansas. The latter Workshop was organized by F. P. L. Marques at the University of São Paulo. The global community of Cestodologists also completed a paper (Chervy, 2009) detailing the long-awaited unified terminology for the surface features unique to cestodes known as microtriches under the pseudonym "Lenta Chervy"—a combination of the words "Tape" and "Worms" in Russian—which our global community of Cestodologists typically employs for their collaborative works.

FIELDWORK

The four "host" teams worked independently to identify the geographic regions and specific host groups to target for conducting fieldwork that would supplement material already in hand. In all cases, highest priority was given to major regions in which a particular vertebrate class had not previously been examined for cestodes. Regions known to be home to vertebrate orders, families, or genera containing species that had been reported to host a particular cestode group, but that included many species that had not yet been examined, were also targeted. With a few exceptions, our original plans to conduct combined field trips involving the collection of cestodes from more than one major vertebrate group were generally foiled by difficulties in obtaining collecting permits spanning several major vertebrate groups or, more often, by the logistical inefficiencies presented by the fact that different methods of capture, often in different types of habitats (e.g., forests vs. ocean, etc.), were required to obtain hosts of different vertebrate classes.

The primary localities surveyed by the four "host" teams over the course of the project are summarized in Figure 1. Cestodes were collected from the following 54 countries: Argentina, Australia, Bangladesh, Belize, Brazil, Bulgaria, Cambodia, Canada, Central African Republic, Chile, China, Costa Rica, Czech Republic, Democratic Republic of Congo, Ecuador, Egypt, Ethiopia, Falkland Islands, France, Gabon, Guatemala, Guyana, India, Indonesia, Iran, Italy, Ivory Coast, Kenya, Madagascar, Malawi, Malaysia, Mexico, Mozambique, New Caledonia, Norway, Peru, Philippines, Portugal, Republic of Kazakhstan, Russia, Senegal, Slovakia, Solomon Islands, South Africa, South Korea, Sudan, Taiwan, Thailand, Tunisia, Uganda, United Kingdom, Ukraine, United States (AK, CT, KS, MS, ND, NE, NY, RI, SC, TN, and TX), and Vietnam.

Collecting trips ranged in duration from a few days to several weeks. Field teams varied in size from one to five individuals. All foreign fieldwork was conducted in collaboration with local experts who provided logistical support as well as knowledge of local faunas. Primary local collaborators, by country are as follows: Mostafa Hossain (Bangladesh); Norlan Lamb and Roy Polonio (Belize); Natalia Da Mata Luchetti, Fernando P. L. Marques, Luis Eduardo Tavares, Marcos Tavares, José Luque, and Ricardo Takemoto (Brazil); Pavel Nikolov (Bulgaria); Touch Bunthang (Cambodia); Manigandan Lejeune Virapin (Canada); Francisco Concha, Günther Försterra, Daniel González-Acuña, and Vreni Häussermann (Chile); Dian Gao, Cai Kuizheng, Pin Nie, Gui Tang Wang, Shan Gong Wu, and Bing Wen Xi (China); Tayler Clarke, Ingo Wehrtmann, and Mario Espinoza (Costa Rica); Oscar Carreno and Gabriela Flores (Ecuador); Mohamed Bosseri and Amal Khalil (Egypt); Eshete Dejen Dresilign, Abebe Getuhun Gubale, and Seyoum Mengistou (Ethiopia); Joost Pompert (Falkland Islands); Bernard Marchand (France); Mathieu Bourgarel and Jean-Paul Gonzales (Gabon); Anirban Ash and Pradip K. Kar (India); Asri Yuinar (Indonesia); Razieh Ghayoumi and Masoumeh Malek (Iran); Andrea Gustinelli (Italy); Inza Kone (Ivory Coast); Steven Goodman, Marie Jeanne Raherilalao, Jeanne Rasamy, and Achille Raselimanana (Madagascar); R. Hashim, Susan Lim (late), and R. Ramli (Malaysia); Samuel Bila (Mozambique); Jean-Lou Justine (New Caledonia); Martin Mortenthaler, Aurora Ramírez Aricara, and Lidia Sánchez (Peru); Rafe Brown (Philippines); Graca Costa and Gui Menezes (Portugal); Vladimir Besprovaznnykh, Vladimir Chistyakov, and Alexey Ermolenko (Russia); Rokhaya Sall (Senegal); David Blair, Tingo Leve, and Richard Mounsey (Solomon Islands); Tracey Fairweather and Robert Leslie (South Africa); Ki Hong Kim (South Korea); Zuheir Mahmoud (Sudan); Hsuan-Ching Ho and Hsuan-Wien Chen (Taiwan); Lawan Chanhome (Thailand); Jim Ellis and Andrew Shinn (UK); Olga Lisitsyna and Yuriy Kvach (Ukraine); Michael Barger, Megan Bean, Sara Brant, Isaure de Buron, Anindo Choudhury, Joseph Cook, Stephen Curran, Bryan Frazier, Andrew Hope, David G. Huffman, John M. Kinsella, Robin Overstreet, Eric Pulis, and Jason Weckstein (USA); Tran T. Binh and Vu Quang Manh (Vietnam).

Across these localities, habitats sampled included coniferous forests (North America, South America, and Asia), temperate forests (North America, South America, and Europe), tropical forests (South America, Africa, Southeast Asia, and Australia), grasslands (prairies, pampas, veld, and steppes), polar regions (Svalbard), freshwater wetlands (lakes, ponds, rivers, and streams), inland seas, sea shores, oceanic islands and coral reefs, and the open ocean (epipelagic, mesopelagic, bathypelagic zones, as well as demersal and benthic zones).

At each locality, vertebrate hosts were captured using the method most appropriate for the habitat(s) represented. Terrestrial hosts were generally captured using mist net, snake stick, Sherman trap, pit fall trap, the occasional firearm, or rarely by hand. Aquatic hosts were collected by trawl, hand-line, long-line, gill net, or hand-spear. Institutional Animal Care and Use Committee (IACUC) protocols were generally issued to the leaders of the four "host" teams by their home institutions. In all cases, permission to collect was obtained from relevant authorities and all local laws and regulations were followed.

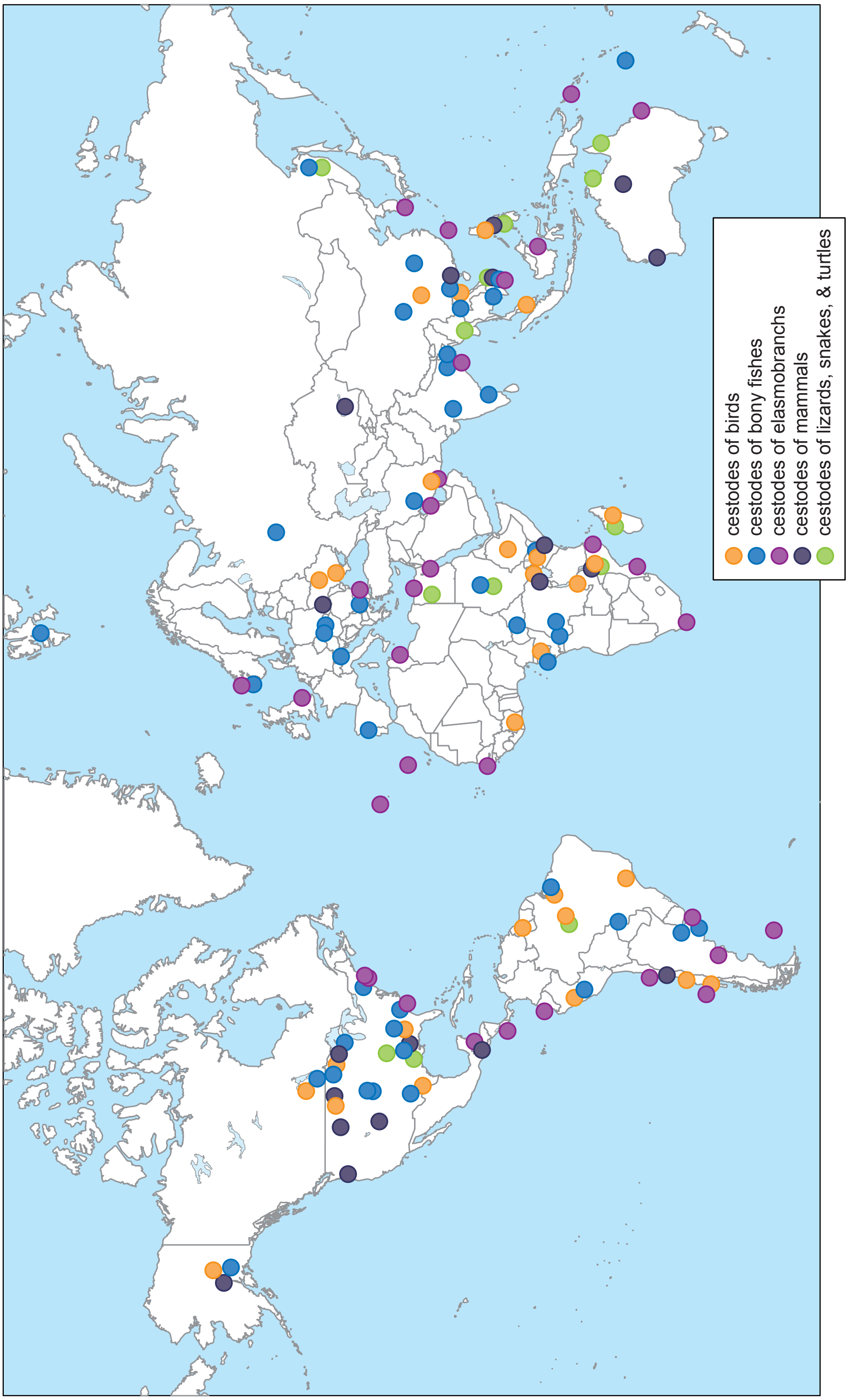

Figure 1. Locations of collecting events and expeditions (by major host group) conducted as part of this PBI project (2008–2017).

In total, 14,884 specimens of 1,906 vertebrate species were examined for cestodes. By major host group, these are as follows: 1,160 specimens representing 143 species of mammals; 3,473 specimens representing 989 species of birds; 219 specimens representing 59 species of snakes, lizards, and frogs; 8,226 specimens of over 500 species of bony fishes; and 1,806 specimens representing 215 species of elasmobranchs. Mammals examined represented approximately 20% of the 139 mammal families, with an emphasis on the Soricomorpha (shrews). Birds examined represented approximately 50% of the 238 bird families, with an emphasis on the Passeriformes. Bony fishes represented approximately 18% of the 497 bony fish families, with an emphasis on Siluriformes and Cypriniformes. Elasmobranch collections represented approximately 40% of the 61 families, with an emphasis on deeper water taxa (e.g., Squaliformes [dogsharks] and Rajiformes [skates]), as well as on groups of Carcharhiniformes [ground sharks], Myliobatiformes [stingrays], and Lamniformes [mackerel sharks] not previously examined for cestodes.

As the title of the project suggests, our focus was on the tapeworms that live in the digestive system of vertebrates. To this end, our collections targeted adult tapeworms in the final (i.e., definitive) host. Tapeworms have wonderfully complex life-cycles, involving at least two, and sometimes three hosts, some of which are also vertebrates, but many of which are invertebrates. It was simply beyond the scope of the project to collect the larval and juvenile stages of tapeworms from these other hosts, although our molecular data tagged to adult vouchers may facilitate identification of many of these in the future.

NOVELTY AND DIVERSITY

Substantial novelty was discovered across a wide array of cestode orders. In total 215 new species were formally described. These included ten or more species in each of the orders Cyclophyllidea (36 new species), Diphyllidea (18 new species), Lecanicephalidea (29 new species), Onchoproteocephalidea I (20 new species), Onchoproteocephalidea II (25 new species), Rhinebothriidea (25 new species), "Tetraphyllidea" relics (10 new species), and Trypanorhyncha (31 new species). In addition, we estimate that material of hundreds of additional new species across orders was collected but remains to be processed. In total, 64 new genera were erected—the majority of these were members of the orders Cyclophyllidea (20 new genera), Lecanicephalidea (9 new genera), Onchoproteocephalidea I (9 new genera), Rhinebothriidea (5 new genera), and Trypanorhyncha (8 new genera).

A substantial body of revisionary work was also completed. In total, 135 new combinations were made across the 19 cestode orders. Major efforts included substantial (almost complete) revisions of the Caryophyllidea and the Bothriocephalidea. Given that most of the questionable species in both orders were originally collected from bony fishes in India and/or Bangladesh, these revisions were made possible through the collection of new material from type hosts in both of these countries. In the end, almost 200 species were synonymized in the Bothriocephalidea (at least 100 species of *Senga*) and Caryophyllidea (86 species).

In combination, the lists of valid taxa for each cestode order provide an informed assessment of the current diversity of cestodes overall. The total number of valid species across the planet today is at least 4,810 (but species are being described monthly so this number is already out of date!), and the total number of valid genera is 833. A breakdown of these totals by cestode order, and by family for the Cyclophyllidea, is provided in Table 1. These numbers do not include the species and genera, listed at the end of each chapter, that are considered *incertae sedis* nor does it include named, but undescribed species and genera that have appeared in molecular phylogenies. Thus, the global fauna of known cestodes is now approaching 5,000 species. The Cyclophyllidea remain by far the most speciose of the 19 cestode orders, with well over 50% of all known cestode diversity, in 437 genera. When numbers are combined for all species, the Onchoproteocephalidea are the second most speciose order, with 562 species, in 79 genera. This order is rivaled only by the Trypanorhyncha in terms of number of genera (i.e., 81), although not in terms of number of species (i.e., 315). Six orders (i.e., the Amphilinidea, Cathetocephalidea, Haplobothriidea, Litobothriidea, Nippotaeniidea, and Spathebothriidea) are on the low end of cestode diversity with less than ten species each. The limited nature of the host associations of each of these groups makes it likely their diversity will not greatly exceed these numbers even with additional collections.

The collection of fresh, properly fixed material led to a much deeper understanding of the morphological complexities of tapeworms. For example, many groups were examined with scanning electron microscopy (SEM) for the first time. Insights into the diversity of scolex configurations seen across tapeworms are provided in the plates of scanning electron micrographs for the following groups: Bothriocephalidea (see fig. 1 in Chapter 3 this volume, Kuchta and Scholz, 2017a), Caryophyllidea (see fig. 3 in Chapter 4 this volume, Scholz and Oros, 2017), Cathetocephalidea (see fig. 1 in Chapter 5 this volume, Caira et al., 2017a), Diphyllidea (see fig. 2 Chapter 7 this volume, Caira et al., 2017b), Diphyllobothriidea (see figs. 1–13 in Chapter 8 this volume, Kuchta and Scholz, 2017b), Haplobothriidea (see fig. 1 in Chapter 10 this volume, Kuchta and Scholz, 2017c), Lecanicephalidea (see fig. 1 in Chapter 11 this volume, Jensen et al., 2017), Litobothriidea (see figs. 2 and 3 in Chapter 12 this volume, Caira et al., 2017c), Nippotaeniidea (see fig. 1 in Chapter 13 this volume, Scholz et al., 2017), Onchoproteocephalidea I (see figs. 8–16 in Chapter 14 this volume, de Chambrier et al., 2017), Onchoproteocephalidea II (see fig. 2 in Chapter 15 this volume, Caira et al., 2017d), Phyllobothriidea (see fig. 1 in Chapter 16 this volume, Ruhnke et al., 2017a), Rhinebothriidea (see fig. 1 in Chapter 17 this volume, Ruhnke et al., 2017b), Spathebothriidea (see fig. 1 in Chapter 18 this volume, Kuchta and Scholz, 2017d), Tetrabothriidea (see fig. 2 in Chapter 19 this volume, Mariaux et al., 2017b), "Tetraphyllidea" relics (see figs. 2–7 in Chapter 20 this volume, Caira et al., 2017e), and Trypanorhyncha (see fig. 1 in Chapter 21 this volume, Beveridge et al., 2017). However, light microscopic work also highly benefited from the collection of newly fixed material as is evident in the beautiful light micrographs provided for the Cyclophyllidea (see figs. 6–21 in Chapter 6 this volume, Mariaux et al., 2017a).

HOST ASSOCIATIONS

Our emphasis on vertebrates in this project is because they, or more specifically their "bowels," *are* the habitat of adult cestodes. Once all vertebrate species on the planet have been examined, the assessment of the global cestode fauna will be complete. However, the daunting nature of that task is illustrated by the magnitude of current estimates of vertebrate diversity: 32,855 species of bony fishes (Eschmeyer and Fong, 2017), 10,404 species of birds (Clements et al., 2016), 10,104 species of snakes and lizards (Uetz, 2017), 7,621 species of amphibians, 5,416 species of mammals (Wilson and Reeder, 2005), 1,269 species of elasmobranchs (Eschmeyer and Fong, 2017), 346 species of turtles (Uetz, 2017), and 52 species of holocephalans (Eschmeyer and Fong, 2017). Nonetheless, our estimates of the number of valid cestode species known from each of these major vertebrate host groups, based on type host species, are interesting to consider. In order of decreasing magnitude these are: 1,540 cestode species are described from mammals, 1,639 species from birds, 1,034 species from elasmobranchs, 465 species from bony fishes, 97 species from snakes and lizards (i.e., squamates), 24 species from amphibians, 11 species from holocephalans, and four species from turtles.

TABLE 1. Number of valid genera and species, and major vertebrate groups parasitized by each cestode order (incl. families for cyclophyllideans only); citation for each chapter treating the respective cestode order is also given. * Major host groups listed in order of decreasing cestode diversity; minor host groups enclosed in parentheses. † Number of species of *Mesocestoides* according to Chertkova and Kosupko (1978).

Cestode group	Major vertebrate host group*	No. of valid genera	No. of valid species	Source
Amphilinidea	bony fishes, turtles	6	8	Scholz and Kuchta (2017) (Chapter 2 this volume)
Bothriocephalidea	bony fishes	48	132	Kuchta and Scholz (2017a) (Chapter 3 this volume)
Caryophyllidea	bony fishes	42	122	Scholz and Oros (2017) (Chapter 4 this volume)
Cathetocephalidea	elasmobranchs	3	6	Caira et al. (2017a) (Chapter 5 this volume)
Cyclophyllidea	birds, mammals, lizards & snakes, (amphibians)	437	3,034	Mariaux et al. (2017a) (Chapter 6 this volume)
Acoleidae Fuhrmann, 1899	birds	2	5	
Amabiliidae Braun, 1900	birds	10	32	
Anoplocephalidae Blanchard, 1891	mammals, lizards & snakes, birds	81	480	
Catenotaeniidae Spasskii, 1950	mammals	6	36	
Davaineidae Braun, 1900	birds, mammals	37	450	
Dilepididae Fuhrmann, 1907	birds, mammals	90	750	
Dioicocestidae Southwell, 1930	birds	5	21	
Dipylidiidae Railliet, 1896	mammals	3	15	
Gryporhynchidae Spasskii & Spasskaya, 1973	birds	16	76	
Hymenolepididae Perrier, 1897	birds, mammals	130	923	
Mesocestoididae Perrier, 1897	mammals, birds	2	13†	
Metadilepididae Spasskii, 1959	birds	10	15	
Nematotaeniidae Lühe, 1910	amphibians	5	19	
Paruterinidae Fuhrmann, 1907	birds, (mammals)	24	125	
Progynotaeniidae Fuhrmann, 1936	birds	6	24	
Taeniidae Ludwig, 1886	mammals	4	50	
Diphyllidea	elasmobranchs	6	59	Caira et al. (2017b) (Chapter 7 this volume)
Diphyllobothriidea	mammals	18	70	Kuchta and Scholz (2017b) (Chapter 8 this volume)
Gyrocotylidea	holocephalans	1	10	Kuchta et al. (2017) (Chapter 9 this volume)
Haplobothriidea	bony fishes	1	2	Kuchta and Scholz (2017c) (Chapter 10 this volume)
Lecanicephalidea	elasmobranchs	29	90	Jensen et al. (2017) (Chapter 11 this volume)
Litobothriidea	elasmobranchs	1	9	Caira et al. (2017c) (Chapter 12 this volume)
Nippotaeniidea	bony fishes	1	6	Scholz et al. (2017) (Chapter 13 this volume)
Onchoproteocephalidea				
Onchoproteocephalidea I	bony fishes, lizards & snakes, amphibians, (turtles), (mammal)	68	316	de Chambrier et al. (2017) (Chapter 14 this volume)
Onchoproteocephalidea II	elasmobranchs	11	246	Caira et al. (2017d) (Chapter 15 this volume)
Phyllobothriidea	elasmobranchs, (holocephalans)	24	69	Ruhnke et al. (2017a) (Chapter 16 this volume)
Rhinebothriidea	elasmobranchs	22	136	Ruhnke et al. (2017b) (Chapter 17 this volume)
Spathebothriidea	bony fishes	5	6	Kuchta and Scholz (2017d) (Chapter 18 this volume)
Tetrabothriidea	birds, mammals	6	70	Mariaux et al. (2017b) (Chapter 19 this volume)
"Tetraphyllidea" relics	elasmobranchs	25	104	Caira et al. (2017e) (Chapter 20 this volume)
Trypanorhyncha	elasmobranchs	81	315	Beveridge et al. (2017) (Chapter 21 this volume)
	TOTAL	**833**	**4,810**	

With 1,034 cestode species described from a host group that includes only 1,269 species, clearly, elasmobranchs were found to play a surprisingly more prominent role as hosts of cestode diversity than anticipated, given their low diversity relative to that of other major vertebrate groups. The disproportionate richness of elasmobranch cestodes is also evident from the number of new species described over the PBI project. Of the 215 new species, 148 (69%) came from elasmobranchs. This is despite the fact that of the 14,884 specimens of 1,906 species of vertebrates examined over the course of the project, only 1,806 specimens (i.e., 12%) of 215 species (i.e., 11%) were elasmobranchs. In essence, the discovery of cestode novelty in elasmobranch hosts required substantially less collecting effort than the discovery of novelty in any of the other major host groups. Several factors could account for their disproportionately high diversity. For example, the cestode faunas of elasmobranchs comprise nine of the 19 cestode orders (i.e., the Cathetocephalidea, Diphyllidea, Lecanicephalidea, Litobothriidea, Onchoproteocephalidea II, Phyllobothriidea, Rhinebothriidea, "Tetraphyllidea" relics, and Trypanorhyncha). The only other vertebrates that rival elasmobranchs in this respect are the bony fishes, which collectively host members of seven cestode orders (i.e., the Amphilinidea, Bothriocephalidea, Caryophyllidea, Haplobothriidea, Nippotaeniidea, Onchoproteocephalidea I, and Spathebothriidea). However, in total, the nine orders in elasmobranchs include 1,034 species, whereas the seven orders in bony fishes include a total of only 465 species. Furthermore, whereas only three of the seven orders parasitizing bony fishes house more than 50 species, seven of the nine orders parasitizing elasmobranchs exceed this number and thus it is commonplace to find representatives of multiple, and in the cases of some stingrays, up to five, orders parasitizing the same species. Alternatively, given their relatively low diversity (i.e., 1,269 species), it is possible that elasmobranchs have simply been more thoroughly sampled than the other vertebrate groups. Indeed, we estimate that over 40% of elasmobranch species have been examined for cestodes. Unfortunately, comparative assessments are not currently available for mammals, birds, or bony fishes owing to their extremely high numbers of species.

We have taken advantage of the tractable nature of elasmobranchs to provide estimates of total global diversity for eight of the nine chapters treating elasmobranch cestodes based on data from both described and undescribed species. We believe these estimates are reasonable not only because of our relatively representative sampling across elasmobranch genera, but also because most species of elasmobranch cestodes exhibit oioxenous specificity for their hosts (*sensu* Euzet and Combes [1980]) in that each generally parasitizes only a single species of host. As a consequence, extrapolation from examined host species to unexamined host species is viable. The estimated total across these eight orders of cestodes parasitizing elasmobranchs is 3,857 species in the 1,269 species of elasmobranchs known. The somewhat more relaxed degree of host specificity seen in the trypanorhynchs (Palm and Caira, 2008) made estimation in that order more difficult. However, if we conservatively assume that on average a single species of trypanorhynch will be found parasitizing each elasmobranch species—which seems reasonable given that it is commonplace for more than a single species of trypanorhynch to parasitize the same host species—the global estimate for trypanorhynchs would be 1,269 species. This would bring the total for all nine orders of cestodes parasitizing elasmobranchs to 5,126.

Extending the above calculations to include all vertebrates so as to generate an estimate of the global cestode fauna overall is complicated by factors beyond the challenges of assessing the proportion of species examined to date for the highly speciose groups of vertebrates. Key among them is the fact that cestodes differ substantially in terms of their degree of host specificity.

While some cestodes exhibit strict specificity for their hosts, host specificity in others is much more relaxed, ranging from mesostenoxenous, to metastenoenous, or even to euryxenous (*sensu* Caira et al. [2003]). This renders a precise global diversity calculation impossible in the absence of detailed host specificity data. Nonetheless, we would offer the following estimate. The subset of the planet's 68,067 vertebrate species that have been examined, are known to host 4,810 species of cestodes. Based on their examination of a total of 3,473 specimens of 989 species of birds, Mariaux et al. (2017a, Chapter 6 this volume) estimated a global total of 8,000 species of cestodes in birds. We estimate the world's elasmobranchs collectively host 5,126 cestode species. Thus, a global cestode fauna of 20,000 species does not seem unrealistic.

As predicted at the inception of the project, a good proportion of cestode novelty was discovered in species that belong to host orders, families, or genera with species known to host other cestodes, but that had not yet been examined for cestodes. However, some unexpected novel host associations were documented. For example, bothriocephalidean cestodes were discovered for the first time from the order Lepisosteiformes (i.e., gars) (Brabec et al., 2015) and also from several families of teleosts not previously known to host this order of cestodes. Onchoproteocephalidea I were reported for the first time from the families Gekkonidae (i.e., geckos) (Coquille and de Chambrier, 2008) and Dactyloidae (i.e., anoles) (Coquille and de Chambrier, 2008). The cestode faunas of deepwater sharks were found to be especially depauperate in terms of diversity, prevalence, and intensity of infections (Caira and Pickering, 2013). Discoveries of novel host associations were generally independent of country, although some surprises, such as a remarkably high amount of cyclophyllidean cestode diversity in the birds of Chile, were encountered. Beyond host type, more important considerations, included for example, habitat type.

Rigorous parasite survey work requires the accurate identification of each and every vertebrate specimen examined, and given prevalence of infection is rarely 100%, and varies considerably across group, examination of multiple specimens of a species is typically required if cestode infections are to be detected. As a consequence, this work can help inform the taxonomy of host groups—especially of groups that are poorly known. This synergy was exemplified by our survey work on the cestodes of elasmobranchs, which had a considerable impact on the taxonomy and systematics of the elasmobranchs themselves. Beyond contributing to a monograph providing NADH2 data for over 4,200 specimens of nearly half of the elasmobranch species known on the planet (Naylor et al., 2012), the project yielded hundreds of tissue samples and images of live or newly sacrificed sharks and rays that were used to inform recent work by elasmobranch taxonomists describing tens of new species and many genera of elasmobranchs (e.g., Last et al., 2016a–c; Manjaji-Matsumoto and Last, 2016). This work in turn has helped to inform fisheries management and conservation efforts focused on these elasmobranch taxa. The elasmobranch team is not unique in this respect. The leaders of all four vertebrate teams are recognized as experts in the taxonomy of their respective vertebrate groups in their own right.

PHYLOGENETICS AND CLASSIFICATION

The highly collaborative nature of the PBI project led to unprecedented advances in our understanding of the phylogenetic relationships and classification of cestodes (see Chapter 22 this volume, Waeschenbach and Littlewood, 2017). Beyond collaborating with one another, taxonomic experts worked closely with molecular phylogeneticists, primarily at the Natural History Museum in London, to generate ordinal-level phylogenetic frameworks. The molecular phylogeneticists were responsible for developing a high-throughput pipeline for the generation of reliable sequence data for multiple genes for nearly 1,000 specimens; these data were complemented by sequence data from large fragments of the mitochondrial genome for representative taxa in 16 of the 19 orders. Taxonomic experts maximized the breadth of taxon sampling in all groups through the collection of new material preserved for molecular work. These individuals ensured the accuracy of the identities of specimens sequenced and, in most cases, prepared hologenophores (*sensu* Pleijel et al., 2008) of specimens sequenced that serve to anchor the identities of these specimens into the future, that were deposited in museums around the world. The large volume of reliable sequence data from accurately identified, vouchered specimens now available in GenBank serves as a valuable resource for those interested in exploring new uses for such data (see Chapter 22 this volume, Waeschenbach and Littlewood, 2017).

The results of these collaborations included phylogenetic frameworks for 14 of the 19 cestode orders. The markers targeted were the two nuclear genes 28S rDNA and 18S rDNA, the two mitochondrial genes COI and 16S rDNA. In total, sequence data for one or more of these genes were generated for over 950 species. The breakdown by gene is as follows: 18S rDNA for 903 specimens, 28S rDNA for 935 specimens, 16S rDNA for 726 specimens, and COI for 829 specimens. Total taxon coverage in these molecular phylogenetic works ranged from 20% (Lecanicephalidea) to 80% (Caryophyllidea) of described species in each order.

Some of the highlights of the insights gained from these comprehensive phylogenetic analyses are as follows. Across the cestodes overall, the non-monophyly of the elasmobranch-hosted order “Tetraphyllidea” was partially resolved by revision of existing ordinal-level classification of the cestodes. To help resolve the situation, the Rhinebothriidea, Phyllobothriidea, and Onchoproteocephalidea were erected as new orders (see Healy et al., 2009; Caira et al., 2014). To preserve the monophyly of all cestode orders, the latter was circumscribed to include both a subset of genera previously assigned to the elasmobranch-hosted tetraphyllidean family Onchobothriidae as well as all species formerly assigned to the order Proteocephalidea, the majority of which parasitize teleosts and herptiles. As a consequence, 19 orders of cestodes are now recognized. Absolutely no support for the monophyly of the group traditionally referred to as the Cestodaria, comprising the orders Amphilinidea + Gyrocotylidea, was seen in analyses in which data for these taxa were included from GenBank and thus we have avoided use of the term Cestodaria here. In contrast the monophyly of the remaining 17 orders (collectively referred to as the Eucestoda) to the exclusion of the Amphilinidea and Gyrocotylidea was highly supported.

Novel phylogenetic frameworks were generated for the Bothriocephalidea, Caryophyllidea, Cyclophyllidea, Diphyllidea, Diphyllobothriidea, Lecanicephalidea, Litobothriidea, Onchoproteocephalidea, Phyllobothriidea, Rhinebothriidea, “Tetraphyllidea” relics, and Trypanorhyncha. In several cases these analyses led to major revisions in classification. The order Trypanorhyncha was subdivided into the two new suborders Trypanobatoidea and Trypanoselachoidea—the former primarily parasitizing batoids as definitive hosts and the latter primarily parasitizing sharks (Olson et al., 2010). Complete family-level classifications were established for the Rhinebothriidea (see Ruhnke et al., 2015) and Lecanicephalidea (see Jensen et al., 2016) for the first time. In the former case two new families (the Anthocephaliidae Ruhnke, Caira & Cox, 2015 and Escherbothriidae Ruhnke, Caira & Cox, 2015) were erected; in the latter case four new families (the Aberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, Eniochobothriidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, Paraberrapecidae Jensen, Caira, Cielocha, Littlewood & Waeschenbach, 2016, and Zanobatocestidae Jensen, Caira, Cielocha, Littlewood

& Waeschenbach, 2016) were erected. The new family Rhoptrobothriidae Caira, Jensen & Ruhnke, 2017 is established within the "Tetraphyllidea" relics, in the present volume (Chapter 20 this volume, Caira et al., 2017e) for a bizarre group of cestodes that parasitizes eaglerays. The new subfamily Testudotaeniinae de Chambrier, Coqille, Mariaux & Tkach, 2009 was established for a group of onchoproteocephalideans from turtles (de Chambrier et al., 2009).

The remarkably beneficial nature of these partnerships is clear from the breadth and depth of the resulting analyses. These works serve to illustrate the remarkable synergism that can arise from interactions between individuals with the combinations of expertise. Many of these collaborations are likely to continue well into the future.

DISSEMINATION

The Global Cestode Database (GCD) (www.tapewormdb.uconn.edu), originally developed as part of a Partnership for Enhancing Expertise in Taxonomy (PEET) project in a FileMaker Pro platform, was transferred to an on-line MySQL platform over the course of the project so as to make the data it houses easily, freely available to the public. Substantial effort was invested in populating this database, which now houses taxonomic information and, in most cases also images, of 12,225 nominal cestode taxa (i.e., including synonyms, etc.). The GCD now serves as the main repository for housing comprehensive information on tapeworm taxonomy and systematics. It has been embraced by the global community of Cestodologists as the key resource for taxonomic and systematic work on tapeworms. Our biggest challenge, now that the PBI project has come to completion, is to develop a sustainable strategy for continuing the population of the GCD into the future so as to keep it current.

On-line MySQL specimen databases were developed *de novo* for each of the major groups of vertebrate hosts. The Elasmobranch Host Specimen Database (www.elasmobranchs.tapewormdb.uconn.edu) is particularly active and now houses data, and in most cases also images, of over 9,200 specimens of sharks and stingrays.

The project website (www.tapeworms.uconn.edu) has served, and given an agreement with the University of Connecticut to maintain the website into perpetuity, will continue to serve as the primary site for the electronic dissemination of the main results of the project. This site also serves as a portal to the GCD and the host specimen databases. The site also provides (i) a list of participants, (ii) information and images of field trips and project meetings and cestode workshops, (iii) a list of new taxa and synonymies resulting from the project, (iv) a list of the publications resulting from the project, (v) quick references and illustrations to larval, microthrix, and egg terminology, etc., and (vi) an illustrated glossary of tapeworm features (with original, standardized images of each feature) that a number of colleagues from across the globe now use as a resource for teaching.

In total, 220 publications focused on the taxonomy, systematics, phylogenetic relationships, and/or morphological features of cestodes resulted from the project. These were complemented by four additional papers focused on parasites belonging to other groups collected incidentally along with cestodes from hosts examined over the courses of the project. A full list of these publications is provided in the Appendix.

TRAINING

One of the major strengths of the project, and a factor that contributed significantly to its success, was the group of extremely capable, talented postdoctoral fellows, and graduate and undergraduate students that we were able to attract to participate in this research. These individuals were fully engaged in all aspects of the laboratory and field elements of the project.

Beyond the intricacies of the taxonomy and systematics of their respective target cestode groups, these individuals received training in the full complement of modern laboratory methods required to identify and describe tapeworms. Many also acquired skills in molecular and phylogenetic methods. A large number of these trainees were engaged in the preparation of publications describing the results; a number also served as authors of chapters in this Special Issue. These individuals are indicated with symbols in the list of project publications in the Appendix. The Training section below provides additional details.

The project employed a flexible strategy for supporting postdoctoral fellows that would match the needs of the four "host" teams with the interests of each fellow. In the cases of some of the foreign individuals, project funding was supplemented with funds from their own institutions. In total, 14 postdoctoral fellows were members of the project team. As a result of the highly collaborative nature of project personnel, most individuals received a blend of training from both foreign and US taxonomic experts. Most of the postdoctoral fellows were successful at obtaining permanent academic or research positions. Each fellow, his or her primary institution of training, and if different, his or her current place of employment, are as follows: Jitka Aldhoun (Natural History Museum in London), Jan Brabec (Czech Academy of Sciences), Joanna Cielocha (University of Kansas; Rockhurst University), Caroline Fyler (University of Connecticut; Martha's Vineyard High School), Voitto Haukisalmi (Finnish Museum of Natural History), Miloslav Jirků (Czech Academy of Sciences), Roman Kuchta (Czech Academy of Sciences), Arseny Makarikov (Russian Academy of Sciences [Siberian Branch]), Maria Pickering (University of Connecticut; Meredith College), Mikulas Oros (Czech Academy of Sciences; Slovak Academy of Sciences), Martina Orosové (Slovak Academy of Sciences), Anna Phillips (University of Connecticut; Smithsonian Institution), and Aneta Yoneva (Bulgarian Academy of Sciences). The efforts of postdoctoral fellow Andrea Waeschenbach (Natural History Museum in London) were instrumental to the success of the molecular phylogenetic elements of the project. Not only did she work closely with each project team to coordinate work on their respective cestode orders, but she also conducted much of the molecular work for the project. Data for sizeable subsets of additional taxa were generated by postdoctoral fellow Jan Brabec, as well as Co-PI Vasyl Tkach and collaborator Fernando Marques.

In total, 34 graduate students, 18 of whom were from the USA, worked on the project. The home countries of foreign graduate students included Argentina, Australia, Brazil, Bulgaria, Canada, Chile, Czech Republic, Iran, and Switzerland. Following their work on the project, among the US graduate students, four doctoral students accepted postdoctoral fellowships (some continuing on this project) and three are currently completing doctoral degrees; two master's students went on to pursue doctoral degrees, one is a research specialist, and one is a freelance scientific illustrator. Of the foreign students, five currently hold assistant professorships or research positions, and three are postdoctoral fellows; two of the master's students went on to pursue doctoral degrees.

Undergraduate students played an especially key role in the project; 59 students were involved, 45 of whom were from the USA. The 14 foreign students were based in Canada, Costa Rica, the Czech Republic, Germany, Ivory Coast, Madagascar, Senegal, Switzerland, and Tunisia. Beyond providing these students with valuable exposure to research, these students received training that helped prepare them to pursue advanced degrees: ten went on to graduate school, four to law school, four to medical school, one to veterinary school, and one is currently enrolled in a combined MD/Ph.D. program. One of the original undergraduates on the project, Stephen Greiman, completed his graduate training and is now an Assistant Professor at Georgia Southern University.

OUTREACH

Their marvelous beauty, obscure biology, and association with vertebrates make tapeworms ideal organisms for enlightening both children and the general public about some of the less well known organisms of the world. Beyond the project website, we engaged in two endeavors that specifically targeted these audiences. A prototype of a children's book focused on tapeworms was completed (Figs. 2, 3). This book, entitled *Meet the Suckers*, takes children inside the animals that live in a typical public Aquarium, introducing them to the wonders of the tapeworms that live inside the animals of an Aquarium. The story begins when Briar and Jakob, the two children featured in the book, receive a package that contains not only "worm-wear" goggles that allow them to see inside of animals, but also a gut-tube containing a "spokesworm" named Cyri. The children (and their cat Rusty) travel with Cyri to an Aquarium, where they learn all about the biology of the many different kinds of tapeworms that live inside of the various animals in each exhibit which they can "see" with their worm-wear goggles (in the book, these tapeworms are hidden under flaps that children reading the book must lift). In all cases, the tapeworms illustrated are the actual species that parasitize each host animal illustrated. Complete with a glossary and several resource pages (as well as a number of puns to keep adult readers entertained), the book highlights the wondrous nature, rather than the potentially distasteful aspects, of tapeworms. The book is authored by "Lenta Chervy" in recognition of the collaborative nature of its creation.

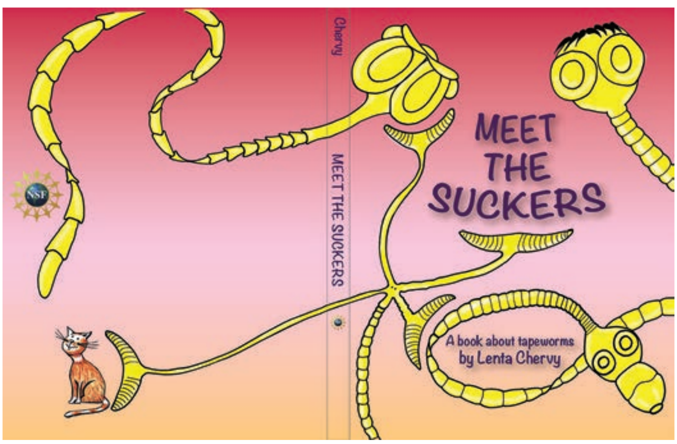

FIGURE 2. Cover design of the prototype of the children's book *Meet the Suckers*.

Aimed at a broader component of the general public, an exhibit entitled "The 'Faces' of Parasites," highlighting some of the results of the project, was developed and installed at the University of Kansas Natural History Museum. This exhibit features four LED panels with 4-foot high, colorized scanning electron micrographs, each of which dramatically portrays the scolex of a different novel tapeworm species discovered over the course of the project. The exhibit is augmented by host and collection visuals displayed on a tablet and actual specimens under a loupe for scale.

FINAL CONSIDERATIONS

This project focused on tapeworms—a gutless group of remarkable parasitic worms found in the digestive system of all major groups of vertebrate animals, including humans. The primary goals of the project were to collect tapeworms from as many different species of mammals, birds, bony fishes, snakes, lizards, turtles, sharks, and stingrays from around the world as possible, to discover and describe as much tapeworm novelty as possible from these hosts, and to establish robust frameworks of the evolutionary relationships of these parasites based on molecular and morphological information. Thanks to the energetic and highly

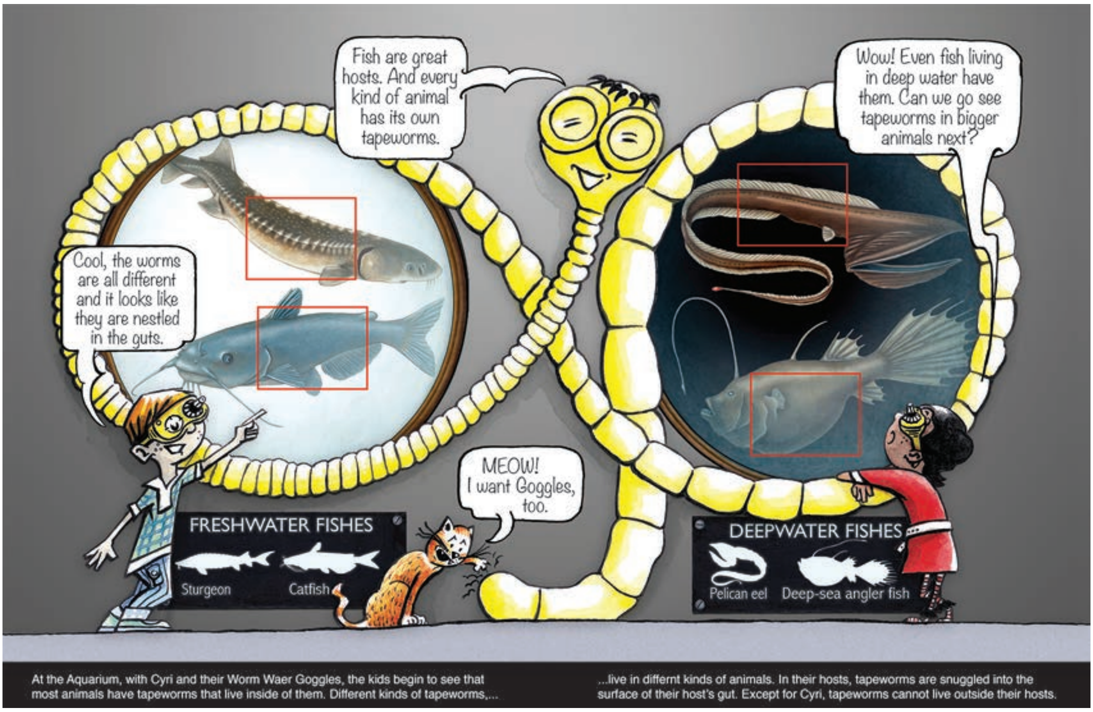

Figure 3. Example spread of the prototype of the children's book *Meet the Suckers* showing the children Briar and Jakob (and Rusty, the cat), accompanied by their "spokesworm" Cyri, at the Aquarium discovering the tapeworms that live inside bony fishes.

collaborative nature the global community of Cestodologists we believe we have exceeded our original goals! The over 210 new species described and over 60 new genera erected bring the global totals to at least 4,810 species and 833 genera. But, this is just the tip of the iceberg!

Our relatively informed estimate of the full magnitude of cestode diversity parasitizing the approximately 68,000 species of vertebrates inhabiting the planet is now a remarkable 20,000 species. As is clear from this estimate, we anticipate that only a subset of vertebrate species will be found to host tapeworms—the results of our survey work provide compelling evidence that vertebrate groups differ substantially in their suitability as hosts for tapeworms. For example, we have learned or, in some cases confirmed, that the following vertebrate groups host few or even no tapeworms. In *mammals* examples of such groups are the Artiodactyla (deer, etc.), Perissodactyla (horses, etc.), and Primata (monkeys, etc.); in *birds* these are the Procellariformes (petrels, etc.) and Sphenisciformes (penguins); in *bony fishes* these are, for example, the Scombridae (mackerels, tunas, etc.); in *elasmobranchs* these are the Squaliformes (dogfish, etc.) and "Scyliorhinidae" (cat sharks). In general the Squamata (snakes and lizards), Chelonii (turtles), and Amphibia (frogs and salamanders) also host few tapeworms. In contrast, the following vertebrate groups appear to be especially good hosts for tapeworms. The *mammal* groups are the Soricomorpha (shrews, etc.), Chiroptera (bats), Lagomorpha (rabbits, etc.), Carnivora (bears, etc.), and Marsupialia (kangaroos, etc.); the *bird* groups are the Passeriformes (sparrows, etc.), Charadriiformes (plovers, sandpipers, seagulls, etc.), Podicipediformes (grebes), and Anseriformes (ducks, geese, swans, etc.); the *bony fish* groups are the Siluriformes (catfish, etc.) and Cypriniformes (carp, etc.); the *elasmobranch* groups are the Myliobatiformes (stingrays, etc.) and Rhinopristiformes (guitarfish, etc.). As tapeworms are transmitted trophically (i.e., through the food web), the intermediate hosts of tapeworms are of particular interest because they can inform biases towards definitive host use.

Because so many of our new tapeworm species were discovered in host species not previously examined for tapeworms, regardless of country, in seeking to discover the remaining approximately two-thirds of the world's global tapeworm fauna, future survey work aimed at discovering additional novelty should focus on unexplored species in these more productive host groups and their close relatives. But, the way forward is not without significant challenges. As highly visible vertebrates, essentially all of these potential host taxa are charismatic creatures. Permits are becoming more difficult to obtain even for the collection of very small numbers of individuals of these taxa. This is unfortunate because, as noted above, tapeworm work has been instrumental in helping to inform the taxonomy and systematics of the vertebrate groups, and as a consequence has also informed policy and conservation efforts aimed at those vertebrate groups. Furthermore, although it is terrific that we now have a relatively robust estimate of the scope of the work required to complete the global picture of tapeworm diversity, the magnitude of that diversity raises important concerns in terms of the future of taxonomic expertise in tapeworms, and of cyclophyllideans in particular. Given the latter order already numbers over 3,000 species, and literally thousands of birds and mammals remain to be surveyed for tapeworms, we anticipate that a large proportion of the estimated 15,000 tapeworm species remaining to be described will likely be cyclophyllideans. In reality, a substantial boost in the number of active tapeworm taxonomists, and especially those working on taxa that parasitize birds and mammals, is required if we are to move forward with achieving the goal of completing the global inventory in a timely fashion. We have contemplated taking a Citizen Science approach to expand the workforce engaged in tapeworm taxonomy, but the challenges of collecting from vertebrates and the expertise required to preserve and prepare tapeworms properly for taxonomic work make this somewhat unrealistic. Reinvigoration of NSF's Partnership for Enhancing Expertise in Taxonomy (PEET) program, which was responsible for training a large proportion of those involved in the elasmobranch tapeworm taxonomy aspects of this project, including one of the PIs, would likely be an effective way to proceed.

The nature of tapeworm taxonomy requires an unusually high degree of methodological rigor when generating molecular sequence data if accurate identities are to be given to the specimens sequenced. Even the largest tapeworm specimens cannot be definitively identified with the naked eye because the majority of the diagnostic features of tapeworms are associated with their internal anatomy. To optimally view these features specimens need to be stained, cleared, and mounted on glass slides. To overcome this problem, project personnel made it a routine practice to sequence only a portion of a tapeworm specimen (usually taken from somewhere on the middle of the strobila) and to prepare the remainder of the specimen (usually scolex and terminal proglottid[s]) for morphological work to serve as a hologenophore to ground the identity of the specimen sequenced. In many instances this practice allowed us to detect issues with identifications when morphological and molecular results conflicted. It is our hope that this practice will be continued into the future for the value of having confirmed identities clearly justifies the extra time and effort required to prepare the hologenophores.

Basic phylogenetic frameworks are now available for most cestode orders. Nowadays, it is unusual to erect new orders of animals, but three new orders were erected between 2009 and 2014 largely as a result of PBI project efforts. As a consequence, ordinal-level classifications have largely been reconfigured to bring them into line with these frameworks, but that work is not yet complete. Much remains to be done with the "Tetraphyllidea" relics before their phylogenetic relationships with respect to one another and other orders are sufficiently well understood to allow a strategy for optimally subdividing them into monophyletic groups can be developed. Further investigation of the phylogenetic relationships of the Phyllobothriidea is likely to necessitate some reconfiguration of this group as well. Serious consideration should be given to establishing the Mesocestoididae as an independent order, given we have shown it to be the sister taxon of a clade that includes both the Cyclophyllidea and the Tetrabothriidea. The family-group level classifications of the Trypanorhyncha and Onchoproteocephalidea are in dire need of attention, as is the genus-level classification of the non-elasmobranch hosted onchoproteocephalideans. Finally, in the cases of most of the 19 orders exhaustive species-level phylogenies are not yet available.

Nonetheless, as a result of PBI project efforts, tapeworms and their vertebrate hosts have emerged as one of the most well-documented host-parasite systems in existence. All sorts of intriguing patterns are beginning to emerge, raising numerous intriguing questions. For example: Why are some groups of tapeworms more host-specific than others? Why do some vertebrate groups make better hosts for tapeworms than others? What circumstances led to the association of tapeworms with humans on more than one occasion over evolutionary time? Are tetrabothriideans essentially just cyclophylideans that parasitize marine mammals? Given that phylogenetic relationships of vertebrate host groups are also more well undestood, rigorous cophylogenetic studies can now be undertaken. Preliminary analyses have already raised a plethora of interesting fundamental questions about the evolution of cestodes and their hosts. For example: What evolutionary processes might account for the fact that, at least in some of the cestodes groups that parasitize elasmobranchs, highly host-specific taxa do not appear to have coevolved with their vertebrate?

Beyond what this system can tell us about the historical associations between tapeworms and their hosts, we hope it serves as a valuable resource for future work investigating the evolution and cophylogenetic relationships of parasites in general, and the processes that govern these associations. We are delighted to have been part of this exciting project and to be able to share our results with others. To this end, a PDF of the entire Special Publication is available at: http://hdl.handle.net/1808/24421 and http://tapeworms.uconn.edu/finalpub.html.

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LITERATURE CITED

Beveridge, I., M. Haseli, V. A. Ivanov, A. Menoret, and B. J. Schaeffner. 2017. Trypanorhyncha Diesing, 1863. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 401–429.

Brabec, J., A. Waeschenbach, T. Scholz, D. T. Littlewood, and R. Kuchta. 2015. Molecular phylogeny of the Bothriocephalidea (Cestoda): molecular data challenge morphological classification. International Journal for Parasitology **45:** 761–771.

Caira, J. N., V. M. Bueno, and K. Jensen. 2017a. Cathetocephalidea Schmidt & Beveridge, 1990. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 65–76.

Caira, J. N., K. Gallagher, and K. Jensen. 2017c. Litobothriidea Dailey, 1969. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 231–241.

Caira, J. N., V. Ivanov, K. Jensen, and F. L. Marques. 2017b. Diphyllidea van Beneden in Carus, 1863. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 149–166.

Caira, J. N., K. Jensen, and K. E. Holsinger. 2003. On a new index of host specificity. *In* Taxonomie, Écologie et Évolution des Métazoaires Parasites. (Livre Hommage à Louis Euzet). Tome 1. C. Combes and J. Jourdane (eds.). PUP, Perpignan, France, pp. 161–201.

Caira, J. N., K. Jensen, and V. Ivanov. 2017d. Onchoproteocephalidea II Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 279–304.

Caira, J. N., K. Jensen, and T. R. Ruhnke. 2017e. "Tetraphyllidea" van Beneden, 1850 relics. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 371–400.

Caira, J. N., K. Jensen, A. Waeschenbach, P. D. Olson, and D. T. J. Littlewood. 2014. Orders out of chaos—molecular phylogenetics reveals the complexity of shark and stingray tapeworm relationships. International Journal for Parasitology **44:** 55–73.

Caira, J. N. and M. Pickering. 2013. Cestodes from deep-water squaliform sharks in the Azores. Deep Sea Research Part II: Topical Studies in Oceanography **98, Part A:** 170–177.

de Chambrier, A., S. C. Coquille, J. Mariaux, and V. Tkach. 2009. Redescription of *Testudotaenia testudo* (Magath, 1924) (Eucestoda: Proteocephalidea), a parasite of *Apalone spinifera* (Le Sueur) (Reptilia: Trionychidae) and *Amia calva* L. (Pisces: Amiidae) in North America and erection of the Testudotaeniinae n. subfam. Systematic Parasitology **73:** 49–64.

de Chambrier, A., T. Scholz, J. Mariaux, and R. Kuchta. 2017. Onchoproteocephalidea I Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 251–277.

Chertkova, A. N. and G. A. Kosupko. 1978. [The suborder Mesocestoidata Skryabin, 1940]. *In* Osnovy Tsestodologii, Volume 9. K. N. Ryzhikov (ed.). Izdatel'stvo Nauka, Moscow, Russia, pp. 118–229. (in Russian).

Chervy, L. 2009. Unified terminology for cestode microtriches: A proposal from the International Workshops on Cestode Systematics in 2002–2008. Folia Parasitologica **56:** 199–230.

Clements, J. F., T. S. Schulenberg, M. J. Iliff, D. Roberson, T. A. Fredericks, B. L. Sullivan, and C. L. Wood. 2016. The eBird/Clements checklist of birds of the world: v2016. http://www.birds.cornell.edu/clementschecklist/download/. Accessed March 2017.

Coquille, S. C. and A. de Chambrier. 2008. *Cairaella henrii* gen. n., sp. n., a parasite of *Norops trachyderma* (Polychrotidae), and *Ophiotaenia nicoleae* sp. n. (Eucestoda: Proteocephalidea), a parasite of *Thecadactylus rapicauda* (Gekkonidae), in Ecuador. Folia Parasitologica **55:** 197–206.

Eschmeyer, W. N. and J. F. Fong. 2017. Catalog of Fishes: Species by family/subfamily. http://researcharchive.calacademy.org/research/ichthyology/catalog/speciesbyfamily.asp. Accessed March 2017.

Euzet, L. and C. Combes. 1980. Les problèmes de l'espèce chez les animaux parasites. *In* Les problèmes de l'espèce dans le règne animal. Mémoires de la Société Zoologique de France **3:** 239–285.

Healy, C. J., J. N. Caira, K. Jensen, B. L. Webster, and D. T. J. Littlewood. 2009. Proposal for a new tapeworm order, Rhinebothriidea. International Journal for Parasitology **39:** 497–511.

Jensen, K., J. N. Caira, J. J. Cielocha, D. T. J. Littlewood, and A. Waeschenbach. 2016. When proglottids and scoleces conflict: phylogenetic relationships and a family-level classification of the Lecanicephalidea (Platyhelminthes: Cestoda). International Journal for Parasitology **46:** 291–310.

Jensen, K., J. J. Cielocha, K. S. Herzog, and J. N. Caira. 2017. Lecanicephalidea Hyman, 1951. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 207–229.

Kuchta, R. and T. Scholz. 2017a. Bothriocephalidea Kuchta, Scholz, Brabec & Bray, 2008. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 29–45.

Kuchta, R. and T. Scholz. 2017b. Diphyllobothriidea Kuchta, Scholz, Brabec & Bray, 2008. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 167–189

Kuchta, R. and T. Scholz. 2017c. Haplobothriidea Joyeux & Baer, 1961. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 201–206.

Kuchta, R. and T. Scholz. 2017d. Spathebothriidea Wardle & McLeod, 1952. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 349–356.

Kuchta, R., T. Scholz, and H. Hansen. 2017. Gyrocotylidea Poche, 1926. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 191–199.

Last, P. R., W. T. White, and P. M. Kyne. 2016a. *Urogymnus acanthobothrium* sp. nov., a new euryhaline whipray (Myliobatiformes: Dasyatidae) from Australia and Papua New Guinea. Zootaxa **4147:** 162–176.

Last, P. R., W. T. White, and G. Naylor. 2016b. Three new stingrays (Myliobatiformes: Dasyatidae) from the Indo-West Pacific. Zootaxa **4147:** 377–402.

Last, P. R., W. T. White, and B. Séret. 2016c. Taxonomic status of maskrays of the *Neotrygon kuhlii* species complex (Myliobatoidei : Dasyatidae) with the description of three new species from the Indo-West Pacific. Zootaxa **4083:** 533–561.

Manjaji-Matsumoto, B. M. and P. R. Last. 2016. Two new whiprays, *Maculabatis arabica* sp. nov. and *M. bineeshi* sp. nov. (Myliobatiformes: Dasyatidae), from the northern Indian Ocean. Zootaxa **4144:** 335–353.

Mariaux, J., R. Kuchta, and E. P. Hoberg. 2017b. Tetrabothriidea Baer, 1954. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 357–370.

Mariaux, J., V. V. Tkach, G. P. Vasileva, A. Waeschenbach, I. Beveridge, Y. D. Dimitrova, V. Haukisalmi, S. E. Greiman, D. T. J. Littlewood, A. A. Makarikov, A. J. Phillips, T. Razafiarisolo, V. Widmer, and B. B. Georgiev. 2017a. Cyclophyllidea van Beneden in Braun, 1900. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 77–148.

Naylor, G. J. P., J. N. Caira, K. Jensen, K. A. M. Rosana, W. T. White, and P. R. Last. 2012. A DNA sequence–based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. Bulletin of the American Museum of Natural History **367:** 1–262.

Olson, P. D., J. N. Caira, K. Jensen, R. M. Overstreet, H. W. Palm, and I. Beveridge. 2010. Evolution of the trypanorhynch tapeworms: Parasite phylogeny supports independent lineages of sharks and rays. International Journal for Parasitology **40:** 223–242.

Palm, H. W. and J. N. Caira. 2008. Host specificity of adult versus larval cestodes of the elasmobranch tapeworm order Trypanorhyncha. International Journal for Parasitology **38:** 381–388.

Pleijel, F., U. Jondelius, E. Norlinder, A. Nygren, B. Oxelman, C. Schander, P. Sundberg, and M. Thollesson. 2008. Phylogenies without roots? A plea for the use of vouchers in molecular phylogenetic studies. Molecular Phylogenetics and Evolution **48:** 369–371.

Ruhnke, T. R., J. N. Caira, and A. Cox. 2015. The cestode order Rhinebothriidea no longer family-less: A molecular phylogenetic investigation with erection of two new families and description of eight new species of *Anthocephalum*. Zootaxa **3904:** 51–81.

Ruhnke, T. R., J. N. Caira, and M. Pickering. 2017a. Phyllobothriidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 305–326.

Ruhnke, T. R., F. B. Reyda, and F. P. L. Marques. 2017b. Rhinebothriidea Healy, Caira, Jensen, Webster & Littlewood, 2009. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 327–348.

Scholz, T., J. Brabec, and R. Kuchta. 2017. Nippotaeniidea Yamaguti, 1939. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 243–250.

Scholz, T. and R. Kuchta. 2017. Amphilinidea Poche, 1922. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 21–28.

Scholz, T. and M. Oros. 2017. Caryophyllidea van Beneden in Carus, 1863. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 47–64.

Uetz, P. (ed.). 2017. The Reptile Database. http://www.reptile-database.org. Accessed March 2017.

Waeschenbach, A. and D. T. J. Littlewood. 2017. A molecular framework for the Cestoda. *In* Planetary Biodiversity Inventory (2008–2017): Tapeworms from Vertebrate Bowels of the Earth. J. N. Caira and K. Jensen (eds.). University of Kansas, Natural History Museum, Special Publication No. 25, Lawrence, KS, USA, pp. 431–451.

Wilson, D. E. and D. M. Reeder (eds.). 2005. Mammal Species of the World. A Taxonomic and Geographic Reference (3rd ed). Johns Hopkins University Press, Baltimore, MD, USA, 2142 pp.